UNIVERSITÉ DU QUÉBEC À MONTRÉAL

INFLUENCE DES CARACTÉRISTIQUES DES MILIEUX FORESTIERS SUR LES DYNAMIQUES DE DÉFOLIATION PAR LA LIVRÉE DES FORÊTS (*MALACOSOMA DISSTRIA* HÜBNER) EN ABITIBI LORS DE L'ÉPIDÉMIE 1999-2002

MÉMOIRE

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CHAPITRE I

Charbonneau, D., F. Lorenzetti, F. Doyon et Y. Mauffette. 2007. «The influence of stand and landscape characteristics on forest tent caterpillar defoliation dynamics: the case of the 1999-2002 outbreak in northwestern Quebec». *en préparation.*

Je suis l'auteur principal de cette publication car j'ai effectué la gestion des bases de données ainsi que les traitements SIG, les analyses, la discussion des résultats et la rédaction de l'article en entier. Les trois coauteurs, soient mon codirecteur Francois Lorenzetti, mon directeur Yves Mauffette et Frederik Doyon ont participé en offrant leurs commentaires et en effectuant les révisions.

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RÉSUMÉ

La forêt boréale renferme plusieurs espèces d'insectes forestiers caractérisés par des dynamiques de population éruptives. Ces insectes peuvent affecter le paysage en influençant la mortalité et la croissance des arbres. La livrée des forêts est un ravageur majeur du peuplier faux-tremble, la plus importante espèce d'arbre feuillu de la forêt boréale de l'Amérique du Nord et une essence qui connaît une importance économique grandissante. Cette étude a pour but d'établir une relation entre les caractéristiques de la végétation forestière et les dynamiques de défoliation de la livrée des forêts lors de l'épidémie de 1999-2002 en Abitibi-Témiscamingue. La végétation forestière est caractérisée par le type d'habitat (forestier, non-forestier), l'âge et le type de couvert de peuplements ainsi que la diversité des types de couverts et l'abondance des milieux de bordure dans le paysage. Ces caractéristiques sont évaluées localement et contextuellement à de multiples étendues spatiales. Les dynamiques de défoliation sont classées en trois catégories de persistance : absence de défoliation, la défoliation modérée ou sévère sur un an et la défoliation modérée ou sévère sur plus d'un an (2-4 ans). Un échantillonnage stratifié aléatoire a été effectué à l'aide d'un système d'information géographique (SIG) à partir d'une base de données géoréférencées contenant les cartes de défoliation et les cartes écoforestières. Des analyses de régressions logistiques nominales ont été utilisées afin de déterminer les probabilités d'incidence des différentes dynamiques de défoliation en fonction des caractéristiques locales et de paysage de la végétation forestière. Les résultats révèlent que les paysages contenant une grande concentration d'essences feuillues où l'âge du peuplement central est de 50 ans sont les plus probables de subir des dynamiques de défoliation prolongées. La diversité des types de couverts dans le paysage augmente la probabilité que les défoliations ne durent qu'une seule année. Une augmentation de l'abondance des milieux de bordure dans le paysage réduit de la persistance de défoliation.

Mots-clés : livrée des forêts, dynamique de défoliation, épidémie, composition forestière, hétérogénéité, régression logistique, Abitibi, boréal

INTRODUCTION

On retrouve dans la forêt boréale plusieurs espèces d'insectes forestiers caractérisés par des dynamiques de population éruptives, c'est-à-dire des espèces qui atteignent occasionnellement de hautes densités sur de larges superficies. Ces insectes peuvent être affectés par la structure du paysage (Roland, 1993). En revanche, ils peuvent également affecter le paysage en influençant la mortalité et la croissance des arbres (Rykiel *et al.*, 1988).

La livrée des forêts (*Malacosoma disstria* Hübner) est un ravageur majeur du peuplier faux-tremble, la plus importante espèce d'arbre feuillu de la forêt boréale de l'Amérique du Nord (Mattson et Addy, 1975). Elle peut être responsable de réductions de croissance annuelle de hauteur et de surface terrière de 72% et 87%, respectivement (Batzer *et al.*, 1995).

Certaines études soutiennent que la mortalité causée par la livrée est négligeable ou se limite aux arbres supprimés (Batzer, 1972; Duncan et Hodson, 1958; Hildahl et Reeks, 1960; Kulman, 1971) tandis que d'autres études démontrent que la durée de la défoliation (Brandt *et al.*, 2003; Cobbold *et al.*, 2005) et l'intensité de la défoliation (Churchill *et al.*, 1964) peuvent influencer la mortalité. Batzer *et al.* (1995) indiquent que la mortalité causée par la livrée peut réduire la densité et la surface terrière jusqu'à 41% et 27% respectivement. Une étude récente (Marchand *et al.*, en préparation) présente des résultats similaires pour la région concernée, soit la forêt boréale méridionale du Québec.

De plus, à notre connaissance, très peu de recherche a été effectuée au niveau de la susceptibilité des peuplements à la livrée, en comparaison aux études portant sur d'autres espèces d'insectes forestiers. En 1993, Roland a publié un article clé sur la relation entre la fragmentation et la durée locale d'une épidémie et une série de

travaux sur le sujet ont suivis (Cooke et Roland, 2000; Fortin et Maufette, 2001; Levesque *et al.*, 2002; Roland, 2005; Roland et Kaupp, 1995; Roland et Taylor, 1997; Rothman et Roland, 1998). Ces études discutent des multiples façons dont la fragmentation pourrait influencer les populations de livrée ainsi que les causes possibles de ces impacts.

Un retard a été accumulé au niveau de l'étude de la susceptibilité des forêts à la livrée par rapport à d'autres insectes forestiers et il a grand besoin d'être rattrapé. Il est important de bien comprendre les facteurs qui influencent la dynamique de population de la livrée des forêts car cela permettrait de faire un meilleur aménagement de la forêt et réduire la mortalité causée par la livrée. On dit même qu'une réduction d'une seule année de défoliation lors d'une épidémie pourrait augmenter la production ligneuse de 10% sur une période d'un cycle épidémique de 10 ans (Anonyme, 1991).

Un examen détaillé de la distribution spatiale de la défoliation causée par la livrée lors de l'épidémie 1999-2002 au Nord-Ouest du Québec a révélé certaines tendances au niveau des dynamiques de population (Charbonneau *et al.*, 2006). Cette étude indique que certains milieux semblent présenter des caractéristiques qui augmentent ou diminuent la probabilité de défoliation. La littérature en matière de susceptibilité[1] et vulnérabilité[2] des peuplements à la défoliation par la livrée indique que très peu de travail a été fait sur le sujet, à l'exception des travaux portant sur la fragmentation, mentionnés plus tôt.

Cependant, plusieurs chercheurs étudiant d'autres espèces d'insectes forestiers (Davidson *et al.*, 2001; Gilpin et Hanski, 1991; Hansson *et al.*, 1995; Kouki *et al.*, 1997) ont démontré que les dynamiques de population étaient affectées par la composition en espèces et l'âge des peuplements ainsi que par l'organisation spatiale

[1] probabilité qu'une population d'insectes atteigne une densité donnée
[2] probabilité d'occurrence de dommages

de ceux-ci à une échelle supra-locale. Il semble très pertinent de voir si ces mêmes caractéristiques jouent également un rôle dans l'établissement de patrons de défoliation pour la livrée. L'étude menée par Kouki *et al.* (1997) examinent également les impacts du paysage sur la vulnérabilité en examinant les caractéristiques des peuplements adjacents.

Comme mentionné plus haut, la durée et l'intensité de la défoliation semblent être de bonnes mesures des dommages occasionnés par la livrée et composeront donc les patrons de défoliation que nous tenterons d'associer aux caractéristiques des peuplements. De façon plus concise, nous voulons établir une association entre des dynamiques de population de la livrée des forêts à travers ses dynamiques de défoliation et des caractéristiques de la végétation forestière, soit (1) l'hétérogénéité du paysage, (2) la composition et la (3) diversité du couvert forestier, et (4) l'âge des peuplements. Nous allons travailler à l'échelle locale et à multiples échelles environnantes.

Diversité, Hétérogénéité, Effet de bordure

Suite à la publication de l'article de Roland en 1993, l'hétérogénéité spatiale, ou l'hétérogénéité du paysage, a reçu beaucoup d'attention en termes de caractéristique environnementale influençant la dynamique de population de la livrée. C'est donc l'aspect pour lequel nous avons le plus d'information en termes de direction de l'interaction ainsi que des mécanismes en jeu.

Ceci fait référence à l'hypothèse de diversité-stabilité émise par Elton (1958) où il avance que la stabilité écologique est dépendante de la diversité biologique. Par la suite, cette hypothèse a stimulé beaucoup de recherche, particulièrement en agriculture (Andow, 1991; Goodman, 1975; Murdoch, 1975), mais également en milieux naturels (Ellner *et al.*, 2001; Levin, 1976; Tilman *et al.*, 1998).

Bergeron *et al.* (1995) rapportent que l'hétérogénéité de la mosaïque forestière semble diminuer la vulnérabilité du sapin baumier (*Abies balsamea*) à la tordeuse des bourgeons d'épinette. Franklin *et al.* (1989) mentionnent que les environnements de composition et/ou de structure mixte encouragent une diversité biologique accrue. De plus, nous savons qu'une grande diversité de prédateurs peut jouer un rôle important de régulation de la dynamique de population d'espèces épidémiques (Schowalter, 1989).

Les mécanismes les plus souvent proposés pour expliquer l'impact des milieux hétérogènes sur les dynamiques de populations vont comme suit :

À petite échelle, il est rapporté que des différences de facteurs physiques entre la bordure et l'intérieur des peuplements (microclimats) pourraient affecter l'herbivore, ses ennemis naturels ou ses plantes hôtes (Roland, 1993; Rothman et Roland, 1998)

À plus grande échelle, on invoque une inhibition du mouvement des parasitoïdes ou de la dissémination de pathogènes viraux causée par la structure du paysage, plus spécifiquement l'hétérogénéité du paysage (Kareiva, 1987; Reeve, 1988). Il est mentionné que l'hétérogénéité spatiale pourrait modifier des processus populationnels, tels que la dispersion et la quête de nourriture chez les parasitoïdes diptères (Roland et Taylor, 1997) ou la transmission de virus (Roland et Kaupp, 1995; Rothman et Roland, 1998).

Parasitisme et Maladie

En 1997, Roland et Taylor ont observé une réduction du taux de parasitisme de la livrée en milieux fragmentés. Au moins quatre espèces de parasitoïdes, dont *Arachnidomyia aldrichi*, démontraient une réduction significative du parasitisme en milieux fragmentés. La mouche parasitoïde *Arachnidomyia aldrichi* est d'un intérêt particulier car elle agit comme vecteur du virus de la polyhédrose nucléaire (VPN) et

nous savons que le déclin de la densité de population lors d'une épidémie est souvent associé à la mortalité causée par ce virus (Clark, 1958; Stairs, 1966) et par la mouche *Arachnidomyia aldrichi* (Hodson, 1939; Hodson, 1941; Hodson, 1977; Sippell, 1962; Witter, 1979). Bien que Roland et Taylor (1997) attribuent les taux de parasitisme réduits à des modifications dans les taux de dispersion des parasitoïdes, ils admettent que des différences microclimatiques en bordure pourraient également jouer un rôle important. En effet, l'importance des conditions microclimatiques en bordure furent mises en valeur lors d'une étude par Rothman et Roland (1998) qui parvinrent à mieux expliquer la performance de colonies de livrée par l'aire des habitats en bordure dans des forêts fragmentées que par la dispersion des parasitoïdes ou des pathogènes.

Effet de bordure

Nous savons qu'il existe des différences microclimatiques, telles que la température de l'air et du sol, l'humidité du sol et surtout les radiations solaires (Brothers et Springarn, 1992; Chen *et al.*, 1993; Kapos, 1989; Oosting et Kramer, 1946; Renhorn *et al.*, 1997; Williams-Linera, 1990), entre les milieux en bordure et au centre des peuplements. Rothman et Roland (1998) ont proposé qu'une augmentation de la lumière dans les milieux à couvert forestier réduit, par exemple les milieux en bordure, pourrait réduire la mortalité par le VPN et donc augmenter la performance des colonies de la livrée. En effet, nous savons que la période pour laquelle un virus demeure infectieux diminue lorsqu'il est exposé à une plus grande radiation solaire, en particulier les ultraviolets (UV). Dans le cas du VPN, Broome *et al.* (1974) trouva que le virus devenait inactif après seulement 10 heures d'exposition directe au soleil.

Nous savons également que des différences dans le régime de lumière ont des impacts sur les caractéristiques physiques, chimiques et morphologiques des plantes (Ashton et Berlyn, 1994; Boardman, 1977; Clough *et al.*, 1979; Dudt et Shure, 1994; Lincoln

et Mooney, 1984; Louda et Rodman, 1996; Mole *et al.*, 1988; Nichols-Orians, 1991). Conséquemment, les milieux en bordure peuvent donc également avoir une influence indirecte sur la dynamique des populations d'insectes phytophages en modifiant la qualité nutritionnelle du feuillage. Une variation dans la qualité de nourriture peut avoir une forte influence sur la croissance et la survie d'insectes immatures (Scriber et Slansky, 1981). Levesque *et al.* (2002) nous indiquent que des individus qui consomment des feuilles exposées au soleil présentent de plus hauts taux de consommation ainsi qu'une plus grande biomasse que des individus qui consomment des feuilles d'ombre. Ils indiquent également que les feuilles exposées au soleil étaient plus facilement digestibles que les feuilles à l'ombre. Certaines études soutiennent même que la qualité nutritive des plantes hôtes chez la génération parentale aurait des effets sur la qualité des œufs qu'ils produisent, ce qui est critique pour la résistance aux maladies de leur progéniture (Rossiter, 1994).

Composition du couvert forestier

Préférences alimentaires de la livrée

Dans la littérature, il est rapporté que la livrée des forêts est un insecte polyphage. On mentionne toutefois certaines tendances générales de préférences alimentaires. La première et plus évidente distinction que l'on peut faire est sa préférence pour les feuillus par rapport aux résineux (Batzer et Morris, 1978). On mentionne également que la livrée évite l'érable rouge. Dans un contexte de forêt boréale méridionale, le peuplier faux-tremble est considéré l'hôte préféré (Anonyme, 1975; Batzer et Morris, 1978), quoique certaines études (Dubuc, 1996; Lareau, 1997; Leblanc, 1999) démontrent également une préférence pour le bouleau blanc.

Connaissances Actuelles

Plusieurs études discutent de l'effet de la composition forestière des peuplements sur les dynamiques de populations d'insectes forestiers. Au niveau de la livrée par contre, l'information est plutôt restreinte.

Lors d'une étude portant sur l'influence de la composition des peuplements sur l'intensité de défoliation chez la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana*), MacKinnon et MacLean (2004) mentionnent que l'intensité de défoliation semble être moins élevée dans les peuplements mixtes, mais n'avancent pas de mécanismes causant cet effet. Franklin *et al.* (1989) appuient ces résultats et expliquent que les peuplements mixtes réduisent la susceptibilité aux ravageurs en permettant une plus grande diversité d'habitats et donc d'espèces, ce qui en retour permet une plus grande présence de prédateurs. Nous savons qu'une grande diversité de prédateurs peut jouer un rôle important dans la dynamique de population des espèces épidémiques (Schowalter, 1989).

Une portion considérable de théorie écologique promulgue la vision que la densité des populations est reliée à la qualité de l'habitat (Hansson *et al.*, 1995). En effet, Davidson *et al.* (2001) mentionnent que, dans le cas de la spongieuse (*Lymantria dispar*), l'intensité de défoliation augmente lorsque la proportion d'espèces d'hôtes présentes augmente. Cela va dans le même sens que ce qui fut avancé dans les études mentionnées auparavant, soit une diminution de l'intensité de défoliation dans les peuplements mixtes. Nous pensons donc que la proportion d'espèces susceptibles présente, donc de la quantité de ressources disponibles, soit un bon indice d'impact de la composition forestière sur les dynamiques de population. Somme toute, chez la livrée, nous pensons que l'intensité de défoliation devrait augmenter lorsque la proportion d'espèces feuillues présentes augmente.

Au niveau du travail effectué sur la livrée, Roland (1993) mentionne une tendance où l'augmentation de la proportion de peuplier disponible dans le paysage réduit la durée

de l'épidémie. Il émet l'hypothèse que dans les milieux à faible présence de peuplier, l'on trouverait de petites parcelles de peuplier en milieu de forêt continue, dominée par des espèces non hôtes, et cela pourrait avoir l'effet d'isoler la livrée et réduire la mobilité des ennemis naturels ce qui en retour atténuerait la capacité des ennemis naturels à réduire la population de livrée et éventuellement mener à la résorption de l'épidémie locale. Cette inefficacité des ennemis naturels aurait pour effet de prolonger la durée locale d'une épidémie lorsque le peuplier est faiblement présent. Toutefois, une étude sur la tordeuse des bourgeons d'épinette (Cappuccino *et al.*, 1998) comparant une matrice forestière composée d'essences hôtes, des îlots d'essences hôtes dans une matrice d'essences non hôtes et des vraies îles, révèle des taux de parasitisme accrus chez les îlots d'hôtes dans une matrice de non hôtes et ce, pour la majorité des parasitoïdes étudiés.

Âge de peuplement

L'impact de l'âge des peuplements et les mécanismes responsables sont peu connus, particulièrement au niveau de la livrée des forêts. À notre connaissance, il n'existe pas d'étude cherchant à associer la dynamique de population de la livrée à l'âge des peuplements. Il est toutefois possible de trouver de l'information concernant d'autres espèces d'insectes forestiers.

Schowalter (1989) dit que, de façon générale, on trouvera une plus grande diversité et abondance de prédateurs d'insectes dans de vieux peuplements et une plus grande abondance d'insectes herbivores dans de jeunes plantations. Inversement, une étude sur la tordeuse du pin gris (*Choristoneura pinus pinus*) (Kouki *et al.*, 1997) mentionne que les peuplements les plus vieux étaient les plus susceptibles. Il s'agissait par contre d'une étude sur des données descriptives et il leur était impossible d'identifier les mécanismes responsables.

Toutefois, plusieurs études traitant de la problématique de la tordeuse des bourgeons de l'épinette rapportent des différences de chimie foliaire selon l'âge des arbres (Bauce *et al.*, 1994; McCullough et Kulman, 1991). Entre autres, l'on mentionne le ratio azote-tannins et la présence plus ou moins grande de phosphore comme étant responsables de différences dans les taux de croissances relatifs, de la digestibilité du feuillage et de l'efficacité de conversion du feuillage. Dans le cas de la tordeuse, les arbres plus matures semblaient présenter des caractéristiques qui favorisent la croissance des individus. Bien que ces résultats soient obtenus pour d'autres espèces que celles considérées dans la présente étude, nous croyons tout de même que la densité de population locale se verra augmenter lorsque l'âge du peuplement augmente.

Bien que la relation entre la qualité du feuillage pour la livrée des forêts et l'âge du peuplier faux-tremble ne soit pas connue, une étude récente menée au Wisconsin (Donaldson *et al.*, 2006) a établi que les composés secondaires qui affectent négativement le développement de la livrée chez le peuplier faux-tremble diminuent exponentiellement avec l'âge. On peut donc penser, par inférence, qu'une augmentation de l'âge peuplements améliorerait le développement des populations de la livrée des forêts. Cela pourrait se traduire par une augmentation de l'intensité et de la durée des épidémies lorsque l'âge des peuplements augmente.

L'étude de Kouki *et al.* (1997) mentionne également que l'âge des peuplements adjacents, donc la structure spatiale de l'âge des peuplements, semble être un facteur plus important dans la dynamique de population que l'âge du peuplement central. Cette hypothèse est également supportée par Gilpin et Hanski (1991) et Hansson *et al.* (1995).

Ils émettent comme hypothèse que des peuplements matures ayant des peuplements adjacents plus jeunes créeraient un effet de bordure. On pourrait alors suggérer des

mécanismes semblables à ceux passés en revue lorsque nous discutions de l'hétérogénéité, soit des différences dans les régimes de lumière qui occasionnent des différences dans la qualité de la nourriture et dans l'efficacité du VPN.

Dans le cadre de cette étude, nous désirons établir une relation entre les caractéristiques locales et supra-locales de la végétation forestière et les dynamiques de population de la livrée des forêts. Nous envisageons atteindre ce but en établissant une association entre des dynamiques de défoliation de la livrée des forêts, soit une combinaison de la persistance et de l'intensité des défoliations, et des caractéristiques des milieux défoliés, soit (1) l'hétérogénéité du paysage, (2) la composition et (3) la diversité du couvert forestier, et (4) l'âge des peuplements. Dans le cas des caractéristiques de peuplements (composition en espèces et âge des peuplements), nous nous intéressons à l'influence des caractéristiques locales sur les dynamiques locales ainsi que sur l'influence des caractéristiques de paysage sur les dynamiques locales.

CHAPITRE I

THE INFLUENCE OF STAND AND LANDSCAPE CHARACTERISTICS ON FOREST TENT CATERPILLAR DEFOLIATION DYNAMICS: THE CASE OF THE 1999-2002 OUTBREAK IN NORTHWESTERN QUEBEC

ABSTRACT

The boreal forest harbors many species of insects characterized by eruptive population dynamics. These insects are known to affect the landscapes they inhabit by influencing tree mortality and growth. The forest tent caterpillar (*Malacosoma disstria* Hübner) is considered a major pest of trembling aspen (*Populus tremuloides*), the most abundant species of deciduous tree within the North American boreal forest. This study aims at establishing a relationship between forest vegetation characteristics and forest tent caterpillar defoliation dynamics. These characteristics are: type of habitat (forested/non forested), stand age and cover type, diversity of cover types and abundance of edge habitats. Stand age and cover type are evaluated locally as well as contextually in the landscape at multiple spatial scales. The remaining characteristics are solely evaluated contextually. Defoliation dynamics are classified into three levels of persistence: absence of defoliation, a single year of moderate to severe defoliation and multiple years of moderate to severe defoliation. Nominal logistic regressions of a stratified random sampling of GIS ready defoliation and ecoforestry databases were used to estimate the probability of occurrence of defoliation dynamics. Results indicate that landscapes containing a high proportion of deciduous species, where the central stand is aged 50 years are most likely to be defoliated. Diversity of landscape cover types increases the probability of being defoliated a single year. A high abundance of edge habitats in the landscape reduces defoliation persistence.

Key words: forest tent caterpillar, defoliation dynamics, outbeak, forest composition, heterogeneity, logistic regression, Abitibi, boreal

1.1 Introduction

In the boreal forest, there are many species of insects characterized by eruptive population dynamics. These are insects that occasionally reach high population densities over large areas. Although these insects are known to be affected by landscape structure (Roland, 1993), they can also affect the very landscapes they inhabit by influencing tree mortality and growth (Rykiel *et al.*, 1988).

The forest tent caterpillar (*Malacosoma disstria* Hübner) plays an important role in boreal forest ecosystems. It is considered a major pest of trembling aspen (*Populus tremuloides*), the most abundant species of deciduous tree within the North American boreal forest. Studies indicate that forest tent caterpillar defoliation can reduce annual growth and basal area as well as cause mortality (Batzer *et al.*, 1995; Brandt *et al.*, 2003; Cobbold *et al.*, 2005; Marchand *et al.*, en préparation).

The effects of stand age on defoliation dynamics and the mechanisms involved are little known (Kouki *et al.*, 1997; McCullough and Kulman, 1991; Donaldson *et al.*, 2006). This is especially true for the forest tent caterpillar. To our knowledge, there are no studies which set out to link forest tent caterpillar population dynamics to stand age.

Some information is available on the variation in leaf chemistry of host species in relation to age for the spruce budworm (Bauce *et al.*, 1994; McCullough and Kulman, 1991). These studies report nitrogen-tannin ratios and phosphor content as being the main sources of variation in relative growth, leaf digestibility and foliage conversion efficiency of budworm larvae. They indicate that mature trees seem to present characteristics that favor larval development.

A recent study on trembling aspen (Donaldson *et al.*, 2006) has established that secondary compounds which have an adverse effect on forest tent caterpillars

decrease exponentially as tree age increases. Thus, it is reasonable to put forward that an increase in stand age would result in an improvement of population growth which in turn would translate into increased defoliation intensity and persistence.

The literature reveals that forest tent caterpillars prefer deciduous host species (Batzer and Morris, 1978), though regional preference in host species varies across North America (Stehr and Cook, 1968). In the southern Quebec, trembling aspen (*Populus tremuloides*) and sugar maple (*Acer saccahrum*) are considered the favored hosts (Anonyme, 1975; Batzer and Morris, 1978). Moreover, certain studies underline the importance of white birch (*Betula papyrifera*) as a host species at higher latitudes. In our study area, Northwestern Quebec, maple is not prevalent and so we shall consider aspen and white birch as the preferred hosts. These comprise the large majority of deciduous species within the study area.

Ecological theory dictates that a greater habitat quality generally leads to a greater population density (Hansson *et al.*, 1995). Thus, a greater proportion of deciduous species in the forest cover translates to a greater concentration of host species for the forest tent caterpillar and consequently a greater habitat quality. Characteristics which are favorable to population growth will lead to a higher probability of defoliation occurrence and persistence.

In support of this, Davidson *et al.* (2001) report an increase in defoliation intensity by the gypsy moth (*Lymantria dispar*) when the proportion of host species increases. Furthermore, MacKinnon et MacLean (2004) indicate that defoliation intensity is lower in mixed stands. Franklin *et al.* (1989) indicate that stands of mixed composition can reduce vulnerability by creating a greater diversity of habitats and consequently allow a greater diversity of predators. This result is supported by the meta-analysis undertaken by Jactel and Brockerhoff (2007). This refers to the

diversity-stability hypothesis first exposed by Elton in 1958 which basically states that ecological stability depends on biological diversity.

The diversity-stability hypothesis has stimulated much research, particularly in agricultural settings (Andow, 1991; Goodman, 1975; Murdoch, 1975), although studies in natural settings have also been undertaken (Ellner *et al.*, 2001; Levin, 1976; Tilman *et al.*, 1998). These studies demonstrate that landscape, or spatial, heterogeneity can play an important role in population processes.

Variation in predator-prey interactions is a mechanism which is often invoked to explain the relationship between spatial heterogeneity and population persistence (DeRoos *et al.*, 1991; May, 1978; Murdoch, 1994). Landscape structure, and landscape heterogeneity in particular, could modify population processes such as dispersal or foraging behavior in dipteran parasitoids (Roland and Taylor, 1997) or the transmission of viral pathogens (Roland and Kaupp, 1995; Rothman and Roland, 1998).

Bergeron *et al.* (1995) report that heterogeneity in the forest matrix diminishes balsam fir (*Abies balsamea*) vulnerability to spruce budworm in Northwestern Quebec. Franklin *et al.* (1989) suggest that environments of mixed composition and/or structure encourage a greater ecological diversity. Furthermore, it has been shown that a high diversity of predators can play an important role in controlling population dynamics of outbeak species (Schowalter, 1989).

It has been demonstrated that microclimatic differences exist between stand edge and interior (Renhorn *et al.*, 1997; Oosting and Kramer, 1946; Brothers and Springarn, 1992; Chen *et al.*, 1993; Williams-Linera, 1990; Kapos, 1989). Rothman and Roland (1998) propose that an increase in UV radiations in stand edge would decrease the effectiveness of the nuclear polyhedrosis virus (NPV), which is often associated with the decline from peak population density during a forest tent caterpillar outbreak.

Furthermore, differences in light regime in edge habitats influence foliage quality and, consequently, population performance (Levesque *et al.*, 2002; Scriber and Slansky, 1981; Rossiter, 1994). Foliage in edge environments tend to have a greater nutritional value which could affect growth and survival of immature insects (Scriber and Slansky, 1981). Levesque *et al.* (2002) report that individuals consuming sun-exposed leaves had a greater consumption rate than those consuming shade leaves. Leaves exposed to the sun were also more digestible.

In the context of this study, we shall examine landscape heterogeneity through the abundance of edge habitats in areas surrounding the local dynamic and landscape diversity through the diversity of stand cover types in these same. Based on the diversity-stability hypothesis we predict an increase in landscape diversity will result in reduced defoliation persistence. Based on the documented effects of edge habitats on population dynamics, we predict that increase in the abundance of edge habitats will result in increased defoliation persistence and intensity.

This study evaluates how stand age, forest cover composition and diversity, and abundance of edge influence forest tent caterpillar defoliation dynamics in northwestern Quebec. Resulting empirical relationships will then be used to elaborate a predictive model that would enable planners to make informed forest management decisions in respect to forest tent caterpillar defoliation.

1.2 Methods

1.2.1 Data

The information for both the response and explanatory variables originate from the Quebec Ministry of Natural Resources and Fauna (MRNF), but are the result of different sampling methods. From 1999-2002 inclusively, the MRNF conducted aerial surveys of defoliation. The information was digitized and georeferenced for use with a geographical information system (GIS). Aerial survey data has been corroborated by ground survey data (Bordeleau *et al.*, 2004).

Forest resource inventory (FRI) maps were elaborated through photo interpretation (early 1990's photos, with updates up to 2002). The data was digitized and georeferenced for use with a GIS (Letourneau *et al.*, 2003).

1.2.2 Study Area

The 1999-2002 forest tent caterpillar outbreak in northwestern Quebec was mostly restricted to the Abitibi-Témiscamingue region. Over the course of four years, defoliation spanned over 1.45 million hectares and peaked, in terms of affected areas as well as intensity, in 2001. The area considered in the context of this study was limited to the north and south by the balsam fir – white birch bioclimatic domain, to the west by the Quebec-Ontario border and to the east by the end of the glacial lacustrine plain (fig. 1.1)

The areas affected during the outbreak were more extensive than those included in the study area. However, 64% of all areas which were defoliated during the outbreak are contained within the study area (fig. 1.2).

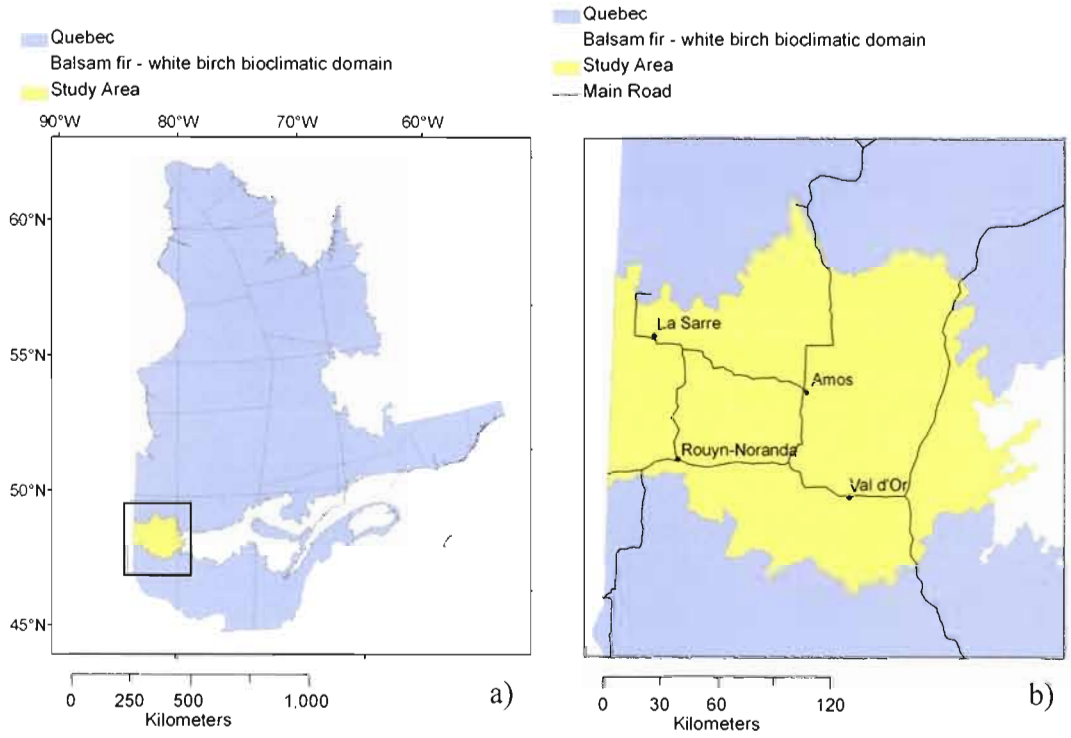


Figure 1.1: Geographic location and extent of the study area. It is limited to the balsam fir – white birch bioclimatic domain, the Quebec-Ontario border to the west and the end of the glacial lacustrine plain to the east

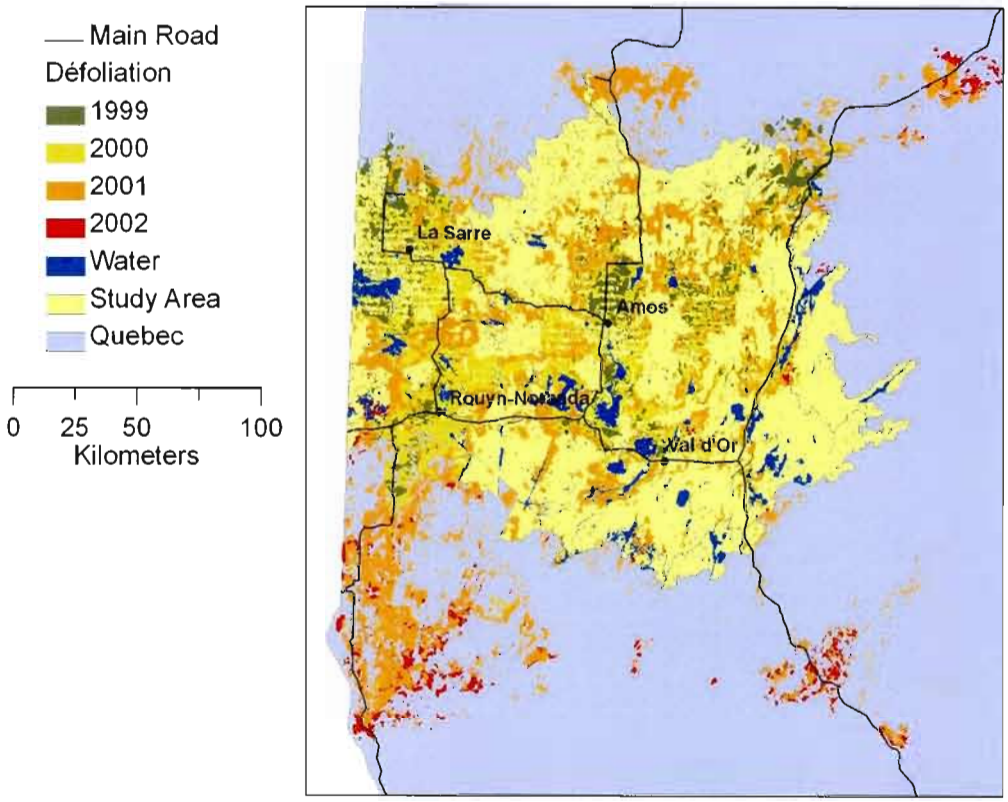


Figure 1.2: Total extent of defoliation surveyed during the 1999-2002 forest tent caterpillar outbreak

Within the study area, the most frequent stand age classes were, in decreasing order, 50 years, 30 years, 70 years, 10 years and 90 years. Predominant stand covers were, in decreasing order, coniferous, deciduous, deciduous mixed and coniferous mixed (See Charbonneau *et al.* (2007) for detailed descriptive statistics of study area structure and defoliation dynamics).

1.2.3 Sampling

Sampling for this study was carried out using ArcGIS (ESRI inc. 2007, Version 9.2) with the georeferenced information layers. The sampling design was a stratified random point sampling. Stratification forces a sufficient representation of all combinations of stand ages and stand cover types. This condition being respected, points were then randomly placed. In order to minimize pseudo-replication, sampling was restricted to one sample point per spatially independent polygon possessing a unique stand age and cover type.

Circular sample areas were delimited around each sample point. In order to determine the range at which variables have the highest explanatory power, buffers of varying radii (500 m, 1000 m, 1500 m and 2000 m) were created. The choice of 2000 m as a maximum radius was a compromise between a sample size sufficient for statistical analyses without overlapping sampled areas, and sufficient variability within the sample area.

The central sample point was used to calculate local characteristics while the circular sample areas around the central point were used to calculate landscape variables (contextual, edge and diversity).

1.2.4 Variables

Variables considered in this study are described in the following section. We have separated the explanatory variables into four classes of variables: local, contextual, edge and diversity variables. A summary of the variables as well as some descriptive statistics can be found in Table 1.1.

It should be noted that, from this point on, areas referred to as being "forested" will be defined as areas possessing an identifiable age class and species code within the MRNF ecoforestry database. Areas referred to as being "non-forested" may be either truly non forested areas or forested areas not possessing an identifiable age class or species code. The latter represents 4.25% of all forested areas.

Table 1.1: Descriptive statistics of all explanatory variables considered in this study

	Variable	Minimum	Average	Maximum	Name	Type
	NDefSev	0.00	0.57	2.00	Defoliation intensity/persistence	Categorical
Local	AGE	10.00	54.03	90.00	Stand age	Categorical
	FMR	1.00	2.53	4.00	Stand cover type	Categorical
	Long	83 209	189 403	308 558	Longitudinal position	Continuous
	Lat	5 281 511	5 375 293	5 480 618	Latitudinal position	Continuous
Contextual	aAge500	10.00	50.99	90.00	Landscape age (500m, 1000m, 1500m and 2000m)	Continuous
	aAge1000	12.17	49.65	88.80		
	aAge1500	11.47	49.13	84.11		
	aAge2000	16.50	48.93	84.26		
	aFMR500	1.00	2.78	4.00	Landscape cover type (500m, 1000m, 1500m and 2000m)	Continuous
	aFMR1000	1.00	2.86	4.00		
	aFMR1500	1.00	2.89	4.00		
	aFMR2000	1.08	2.90	4.00		
	aFnF500	0.07	0.66	1.00	Proportion of forested areas (500m, 1000m, 1500m and 2000m)	Continuous
	aFnF1000	0.07	0.61	1.00		
	aFnF1500	0.10	0.59	0.98		
	aFnF2000	0.09	0.58	0.93		
Edge	eCHa500	0.00	1 952	6 417	Differential stand height edge (500m, 1000m, 1500m and 2000m)	Continuous
	eCHa1000	0.00	7 081	19 455		
	eCHa1500	229	15 337	35 053		
	eCHa2000	1 673	26 397	60 698		
	eFnF500	0.00	3 510	9 491	Forested / Non forested edge (500m, 1000m, 1500m and 2000m)	Continuous
	eFnF1000	0.10	14 081	27 680		
	eFnF1500	2 389	31 559	55 815		
	eFnF2000	15 538	55 828	94 647		
	NLine500	0.00	140	1 813	Road and river edge (500m, 1000m, 1500m and 2000m)	Continuous
	NLine1000	0.00	615	6 526		
	NLine1500	0.00	1 401	10 633		
	NLine2000	0.00	2 446	14 391		
Diversity	hAge500	0.00	0.71	1.38	Diversity of landscape ages (500m, 1000m, 1500m and 2000m)	Continuous
	hAge1000	0.13	0.83	1.46		
	hAge1500	0.24	0.89	1.49		
	hAge2000	0.24	0.92	1.41		
	hFMR500	0.04	0.76	1.37	Diversity of landscape cover types (500m, 1000m, 1500m and 2000m)	Continuous
	hFMR1000	0.13	0.84	1.34		
	hFMR1500	0.16	0.86	1.30		
	hFMR2000	0.19	0.87	1.30		

Local variables

Local variables include stand age, stand cover type, and longitudinal and latitudinal positions. Stand age is evaluated in classes. Each class represents a 20 year age bracket and is coded according to the central value of the bracket (e.g. 1-20 years coded as 10 years). We consider 5 age classes: 1-20 years, 21-40 years, 41-60 years, 61-80 years and 81+ years. In order to remove confounding effects caused by uneven-aged stands, we restrict sampling to even-aged stands. These represent 97.3% of forested stands in the study area.

Stand cover type is based on the dominant and codominant species found in the stands where sample points fell and is divided into four cover types: deciduous (1: 75%-100% deciduous), mixed with dominant deciduous (2: 50%-75% deciduous), mixed with dominant coniferous (3: 25%-50% deciduous) and coniferous (4: 0%-25% deciduous).

Longitudinal and latitudinal positions represent the geographical position of the sample point.

Landscape variables

i) Contextual variables

Landscape age and landscape cover type represent, respectively, the area-weighted average of stand ages and forest cover types of stands in an area of defined radius centered on the sample point. Landscape age varies between 10 and 90 and is evaluated by:

$$\frac{\sum_{j}^{i=0}\left(A_i \times N_i\right)}{N_{Stand}} \qquad \textbf{Eq 1.1}$$

Where :

A_i = Age class within stand i

N_i = Area occupied by stand i within the circular sample area of defined radius

N_{Stand} = Total area occupied by forested stands within the sample area

Landscape cover type varies from 1 to 4 and is evaluated by:

$$\frac{\sum_{j}^{i=0}(C_i \times N_i)}{N_{S\tan d}} \qquad \textbf{Eq 1.2}$$

Where :

C_i = Forest cover type within stand i

N_i = Area occupied by stand i within the circular sample area of defined radius

N_{Stand} = Total area occupied by forested stands within the sample area

A value of 1 indicates that all forested areas within the sampled radius are of a deciduous cover type, while a value of 4 indicates that they are all coniferous. A value of 2.5 is equivalent to half of forested areas being deciduous and the other half coniferous but can be attained through any number of possible combinations of stand cover types.

The proportion of forested to non-forested areas is a simple ratio and, as such, varies from >0 to 1, where a higher value indicates a greater proportion of forested areas within the sample radius. A value of 1 indicates that all areas within the sample radius are forested.

ii) Edge variables

Edge variables are the summation of segment lengths created by the meeting of two different types of areas. We consider three types of edges: (1) forested with non-

forested areas, (2) two neighboring stands of different heights and (3) edges created by the presence of primary or secondary roads or permanent rivers.

iii) Diversity variables

Diversity variables are based upon the Shannon diversity index (Bégon et Harper, 1996). In this study, they will be calculated by:

$$-\sum_{i=1}^{j}(p_i \times \ln p_i) \qquad \textbf{Eq 1.3}$$

Where p_i = Proportion of stand characteristic i

In the case of the diversity of landscape ages, p_i represents the proportion of stands of age i and in the case of diversity of landscape cover types, p_i represents the proportion of areas with cover type i. The diversity variables increase either by having additional unique stand ages/stand cover types present or by having a greater evenness in the stand ages/stand cover types.

Defoliation dynamics

Defoliation dynamics are described by the intensity and persistence of defoliation and, as such, our response variable must include these two dimensions. Defoliation dynamics examined in this study are limited to three combinations of intensity/persistence: absence of defoliation, a single year of moderate or severe defoliation (26-100% canopy defoliation) and two to four years of moderate or severe defoliation.

In areas where moderate or severe defoliations have occurred, light defoliations occurring in the remaining years were ignored. This implies that, except in the cases

where defoliations were moderate to severe for four years, areas that have been defoliated moderately or severely from one to three years may also have been lightly defoliated from one to three years. The occurrence of light defoliations in points defined as having been moderately or severely defoliated represents 7.3% of all sampled points (18.3% of sampled points defined as having been defoliated moderately or severely).

Moderate or severe defoliations lasting from two to four years are grouped together because total areas having been defoliated three years or more are least present in the study area and thus we could not obtain a sufficient sample size for the analyses (Table 1.2).

Qualitative analyses comparing the distributions of stand ages and cover types affected by the forest tent caterpillar have established that little or no variation exists between the areas affected by two, three or four years of moderate or severe defoliation, regardless of having also been lightly defoliated or not. Areas having only been lightly defoliated were eliminated because they too were insufficiently represented. Although Table 1.2 seems to indicate that this would also be the case for areas having been moderately or severely defoliated for a single year, it is important to understand that the area affected by defoliation dynamics is not directly proportional to an amount of spatially independent points.

From this point on, we shall refer to moderate or severe defoliation simply as defoliation. Whenever this is not the case, it shall be clearly stated.

Table 1.2: Total forested areas affected by the different defoliation dynamics within the study area. Absence of defoliation refers to areas having never been inventoried as being defoliated. Light defoliation refers to areas having only been defoliated lightly 1-4 years over the course of the outbreak. The remaining defoliation dynamics refer to areas having been moderately or severely defoliated 1, 2, 3 and 4 years. These areas may have also been lightly defoliated over the course of the outbreak.

Defoliation dynamic	Ha	%
Absence of defoliation	485 327	53.86
Light defoliation (1-4 years)	2 873	0.32
1 year - moderate or severe defoliation	41 253	4.58
2 years - moderate or severe defoliation	217 574	24.15
3 years - moderate or severe defoliation	122 351	13.58
4 years - moderate or severe defoliation	31 736	3.52
TOTAL	**901 115**	**100.00**

1.2.5 Data Analysis

Nominal logistic regressions were used to analyze the data. First, univariate models of each explanatory variable were elaborated in order to observe the direction and importance of their influence on defoliation dynamics. Models incorporating the variables in each variable class (local, contextual, edge and diversity) were then constructed and compared amongst themselves as well as to the univariate models. Finally, the results of the analyses were used to construct a parsimonious predictive model of defoliation dynamics.

In order to compare univariate models and class models, the χ^2 values of the univariate models were compared to the χ^2 statistic obtained. The class model χ^2 statistic is the difference in -2 log-likelihoods between the final model and a reduced model. The reduced model is formed by omitting an effect from the final model. The null hypothesis is that all parameters of that effect are 0.

For all analyses carried out, the reference dependant variable class was the absence of defoliation dynamic. When the independent variables comprised categorical

variables, the last class of the categorical variable was the reference for parameter estimates (i.e. 90 years for stand age and coniferous cover for stand cover type)

For each variable class, variables included in class models were compared to their univariate counterparts. In the case of landscape variables, only one radius for each variable was included. The univariate model radius with the highest χ^2 value was selected. The direction in which variables influence each defoliation dynamic was then observed.

In order to establish the direction in which variables influence defoliation dynamics, the probability of occurrence of each defoliation dynamic in relation to the variables included in the model was calculated by equation 1.4, where n variables may be included in the model.:

$$prob_{1yr} = \frac{(B_{1yr\_Var1} \times B_{1yr\_Var2} \times B_{1yr\_Var\_n} \times B_{1yr\_inter})}{\left(\begin{array}{l} (B_{NoDef\_Var1} \times B_{NoDef\_Var2} \times B_{NoDef\_Var\_n} \times B_{NoDef\_inter}) + \\ (B_{1yr\_Var1} \times B_{1yr\_Var2} \times B_{1yr\_Var\_n} \times B_{1yr\_inter}) + \\ (B_{2yrs\_Var1} \times B_{2yrs\_Var2} \times B_{2yrs\_Var\_n} \times B_{2yrs\_inter}) \end{array} \right)} \quad \textbf{Eq 1.4}$$

Where :

$prob_{1yr}$ = Probability of occurrence of defoliation dynamic 1 year of defoliation

B_{NoDef_Var1} = Parameter estimate of variable 1 for defoliation dynamic absence of defoliation

B_{1yr_Var2} = Parameter estimate of variable 2 for defoliation dynamic 1 year of defoliation

B_{1yr_Varn} = Parameter estimate of variable n for defoliation dynamic 2-4 years of defoliation

It should be noted that the influence of the variables on defoliation dynamics observed through univariate regressions are generally comparable to those obtained with more complex models. For example, if a univariate model describes an increase in probability of defoliation exceeding a single year when landscape age increases,

the same relation should be true when the same variable is included in a multivariable model.

1.3 Results

1.3.1 Sorting out the variables

Local Variables

Univariate models in relation to Class model

The main difference between the univariate models and the class model parameters is the reduction in the explanatory power of the longitudinal variable. Indeed, though the univariate model for longitudinal position obtains a high χ^2 value, a large portion of the explained variability can also be explained by other local variables (Table 1.3).

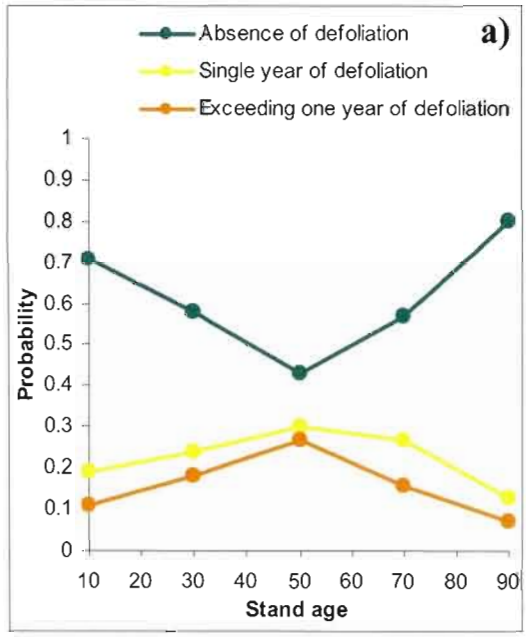
Table 1.3 : Comparison of χ^2 values obtained for univariate models based on local variables and a class multivariate model including all local variables. The final multivariate model χ^2 value may be found in the bottom row

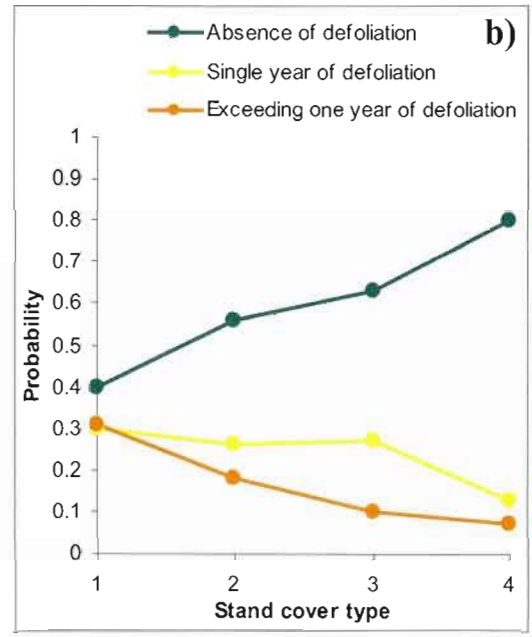
Variable	Univariate models		Local model	
	χ^2	*P*-value	χ^2	*P*-value
Stand age	75.08	<0.0001	64.53	<0.0001
Stand cover type	101.64	<0.0001	96.12	<0.0001
Easting	60.11	<0.0001	23.53	<0.0001
Northing	10.15	0.006	11.24	<0.0001
		Class model	**221.97**	**<0.0001**

Direction of influence

The probability for absence of defoliation is lowest at a stand age of 50 years and increases with when stand age increases or decreases from 50 years (fig. 1.3a). The inverse tendency is observed for the probability of a single or multiple years of defoliation. The distribution is however asymmetrical, there being a greater tendency towards a single year of defoliation in stands of local age 70 years. Overall, a single year of defoliation seems more probable than multiple years of defoliation.

Figure 1.3b indicates a decrease in defoliation probability when the stand cover type tends towards containing a higher proportion of coniferous species. A single year of defoliation is more likely than multiple years in mixed stands (stand cover types 2 and 3).





	Stand age	P-Value
Single year of defoliation	10 yrs	0.134
	30 yrs	0.002
	50 yrs	<0.0001
	70 yrs	<0.0001
	90 yrs	.
Exceeding one year of defoliation	10 yrs	0.146
	30 yrs	<0.0001
	50 yrs	<0.0001
	70 yrs	0.001
	90 yrs	.

	Stand cover type	P-Value
Single year of defoliation	Deciduous	<0.0001
	Mixed - Dominant deciduous	<0.0001
	Mixed - Dominant coniferous	<0.0001
	Coniferous	.
Exceeding one year of defoliation	Deciduous	<0.0001
	Mixed - Dominant deciduous	<0.0001
	Mixed - Dominant coniferous	0.088
	Coniferous	.

Figure 1.3 : Estimated probabilities of defoliation dynamics in relation to a) stand age and b) stand cover type. The probabilities were estimated through univariate models. Parameter P-values can be found in the tables below the figures.

In a model building context

Table 1.3 shows that both stand age and cover type are important variables and should be considered in the final predictive model. As was mentioned previously, the univariate model for longitudinal position obtains a high χ^2 value but a large portion of the variability explained by this variable may also be explained by other local variables and so will not be considered for inclusion in the final predictive model.

Landscape variables

i) Contextual variables

Univariate models in relation to Class model

The contextual class model obtains a χ^2 value similar to that obtained by the univariate model for landscape cover type (1500m) (Table 1.4). This means that a large portion of the variability explained by both the landscape age and the proportion of forested areas can equally be explained by landscape cover type.

Table 1.4 : Comparison of χ^2 values obtained for univariate models of contextual variables and a class multivariate model including all contextual variables. The final multivariate model χ^2 value may be found in the bottom row. For each variable type, only the radius with the highest χ^2 value (in bold) was included in the multivariate model

Variable		Univariate models		Proportion model	
		χ^2	*P*-value	χ^2	*P*-value
Landscape age	500 m	10.67	0.005		
	1000 m	20.84	<0.0001		
	1500 m	25.44	<0.0001		
	2000 m	**28.38**	**<0.0001**	**4.17**	**0.124**
Landscape cover type	500 m	217.32	<0.0001		
	1000 m	245.88	<0.0001		
	1500 m	**261.77**	**<0.0001**	**225.53**	**<0.0001**
	2000 m	261.64	<0.0001		
Proportion of forested areas	500 m	0.25	0.883		
	1000 m	2.92	0.232		
	1500 m	8.91	0.012		
	2000 m	**15.66**	**<0.0001**	**4.24**	**0.120**
			Class model	**270.15**	**<0.0001**

Direction of influence

As observed with stand cover type, the probability of an absence of defoliation increases and the probability of multiple years of defoliation decreases when the proportion of coniferous species in the landscape increases (fig. 1.4). However, the probability of a single year of defoliation is different. The highest probabilities for this dynamic still occur in mixed landscapes, but the probability of a single year of defoliation decreases when the landscape contains a high proportion of deciduous species. This is because of the greater probability of having two or more years of defoliation in these landscapes.

Furthermore, the probability variations are higher in amplitude in this case than they were for stand cover types. For example, the probability for an absence of defoliation varies from 0.4 to 0.8 when stand cover type is the explanatory variable while it varies from 0.04 to 0.9 when landscape cover type is the explanatory variable.

Of particular interest is the fact that the probability for all dynamics are about equal near a value for landscape cover type of 2.2.

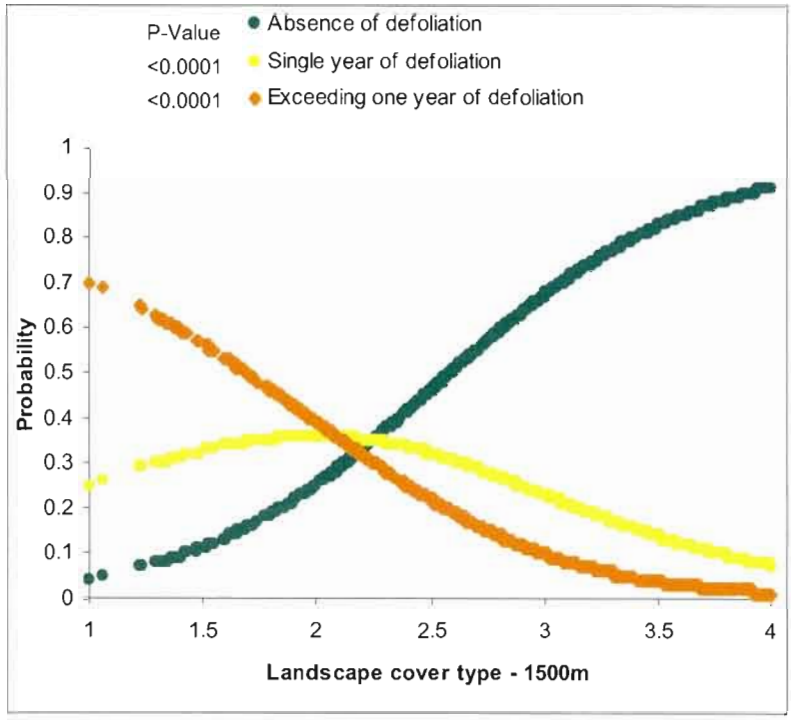


Figure 1.4 : Estimated probabilities of defoliation dynamics in relation to landscape cover type. Probabilities were estimated through a univariate model. Parameter P-values can be found to the left of the legend

In a model building context

In the section dedicated to local variables, it was mentioned that stand cover type should be considered for inclusion in the final predictive model. In this section, we find that landscape cover type is equally interesting and its univariate model obtains a much higher χ^2 value (261.77 vs. 101.64). Further analyses reveal that much of the variability explained by stand cover type can also be explained by landscape cover type. Specifically, a model including both these variables obtains a χ^2 of 273.90 while the univariate landscape cover type model obtains 261.77. Thus, it is more efficient to retain landscape cover type and drop local cover type.

To summarize, variables retained thus far are: stand age and landscape cover type. A model combining only these two variables produces a χ^2 of 315.47 while a model comprising all local and selected landscape variables obtains a χ^2 of 355.52.

ii) Edge variables

Univariate models in relation to Class model

The χ^2 values obtained for the univariate models using the edge class variables are very similar to the χ^2 values obtained for their counterparts in the edge class model (Table 1.5). There seems to be very little redundant information within this class of variables. Unfortunately, χ^2 values for all univariate models are generally low.

Table 1.5 : Comparison of χ^2 values obtained for univariate models of edge variables and a class multivariate model including all edge variables. The final multivariate model χ^2 value may be found in the bottom row. For each variable type, only the radius with the highest χ^2 value (in bold) was included in the multivariate model

Variable		Univariate models		Edge model	
		χ^2	*P*-value	χ^2	*P*-value
Differential stand height edge	500 m	9.75	0.008		
	1000 m	**12.18**	**0.002**	**8.83**	**0.01**
	1500 m	10.32	0.006		
	2000 m	7.18	0.028		
Forested / Non forested edge	500 m	0.43	0.805		
	1000 m	0.71	0.700		
	1500 m	4.22	0.121		
	2000 m	**7.47**	**0.024**	**8.56**	**0.01**
Road and river edge	500 m	8.79	0.012		
	1000 m	9.21	0.010		
	1500 m	16.48	<0.0001		
	2000 m	**18.59**	**<0.0001**	**14.02**	**<0.0001**
			Class model	**34.84**	**<0.0001**

Direction of influence

Independently of the type of border, an increase of landscape contrast in the areas surrounding the central sample point decreases the probability of an absence of defoliation, while it increases the probability of a single year of defoliation (fig. 1.5 a, b, and c). An increase in differential stand height and road and river edge increases the probability of multiple years of defoliation. Forest/non forested edge does not significantly influence the probability of occurrence of multiple years of defoliation (fig. 1.5b).

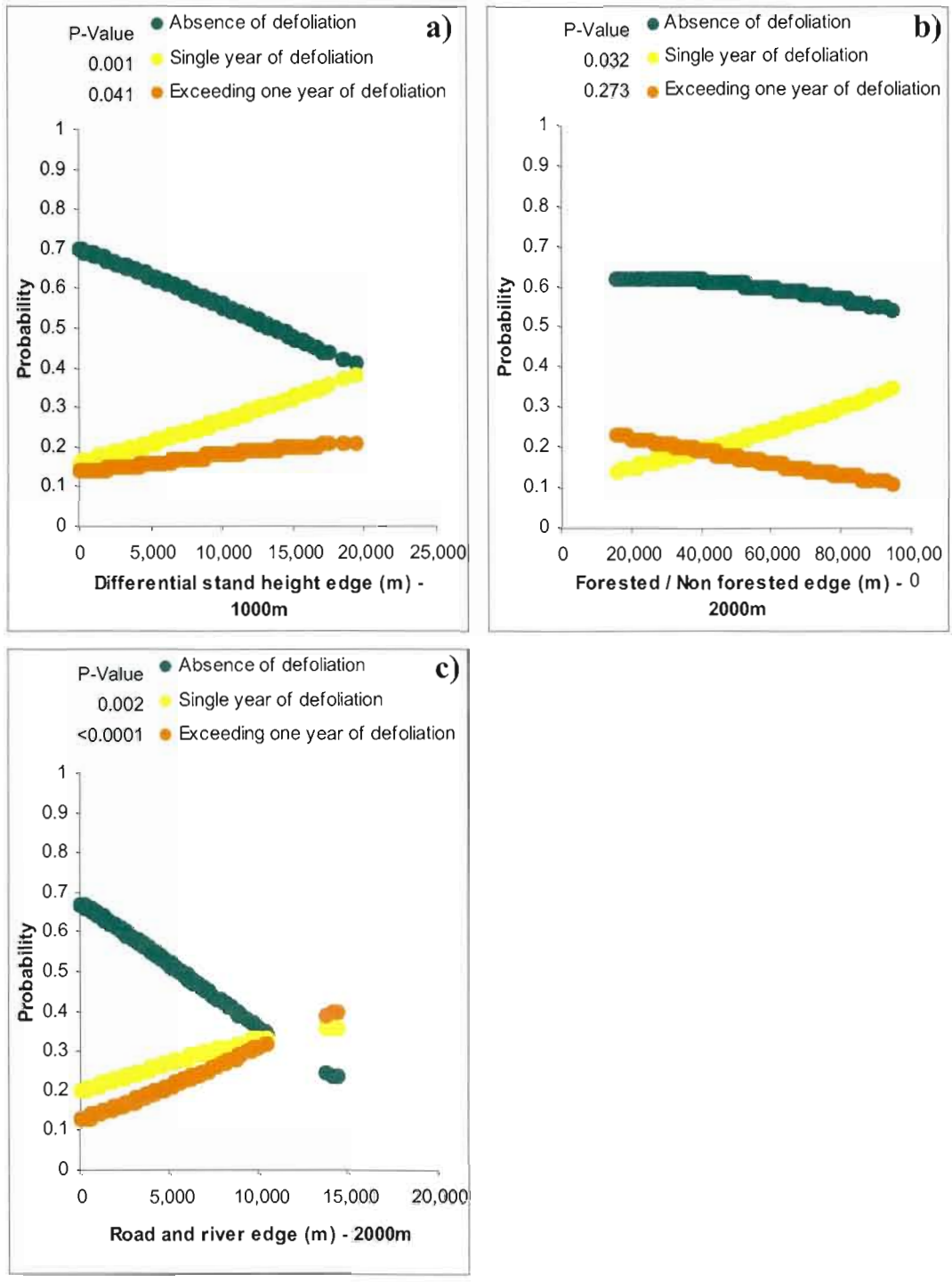


Figure 1.5 : Estimated probabilities of defoliation dynamics in relation to a) differential stand height edge; b) forested/non-forested edge; and c) road and river edge. Probabilities were estimated through univariate models including the relevant variable. Parameter P-values can be found to the left of the legends

In a model building context

For values of forested/non forest edge greater that 40 000 m, the probability of occurrence of one year of defoliation diverges from the probabilities of multiple years of defoliation. This indicates that the inclusion of this variable in the final predictive model could help discriminate between these two dynamics. This is important because, for previous variables, these two dynamics behave much in the same way (fig. 1.3, fig 1.4, fig. 1.5a and fig.1.5c).

iii) Diversity variables

Univariate models in relation to Class model

Though the χ^2 for the diversity of landscape cover types at a radius of 2000m is slightly higher than at 1500m, the latter was selected because landscape cover type and diversity landscape cover types are closely related variables and as such we preferred observing their effects at one single spatial scale.

Furthermore, the χ^2 values obtained for the univariate diversity of landscape ages model is very low, while the univariate diversity of landscape cover types model is very high (Table 1.6).

Table 1.6 : Comparison of χ^2 values obtained for univariate models of heterogeneity variables and a class multivariate model including all heterogeneity variables. The final multivariate model χ^2 value may be found in the bottom row. For each variable type, only the radius with the highest χ^2 value (in bold) was included in the multivariate model (See text for exception – Diversity of landscape cover types)

Variable		Univariate models		Heterogeneity model	
		χ^2	*P - Value*	χ^2	*P - Value*
Diversity of landscape ages	500 m	0.95	0.620		
	1000 m	0.86	0.649		
	1500 m	0.04	0.982		
	2000 m	**2.19**	**0.334**	**3.59**	**0.166**
Diversity of landscape cover types	500 m	30.52	<0.0001		
	1000 m	54.63	<0.0001		
	1500 m*	**71.43**	**<0.0001**	**72.83**	**<0.0001**
	2000 m	72.85	<0.0001		
			Class Model	**75.03**	**0.00**

Direction of influence

The probability of defoliation, for a single year or for multiple years, increases when the diversity of landscape cover types increases. The probabilities of an absence of defoliation and of a single year of defoliation vary rapidly, particularly when diversity is high, while the probability of multiple years of defoliation increases slowly and steadily (fig. 1.6).

As seen with forested/non forested edge, the probability of occurrence of one year of defoliation diverges from the probabilities of multiple years of defoliation diverges when heterogeneity of adjacent area stand cover types is greater that 1. This variable could also be used to discriminate between defoliation dynamics of 1 year and multiple years.

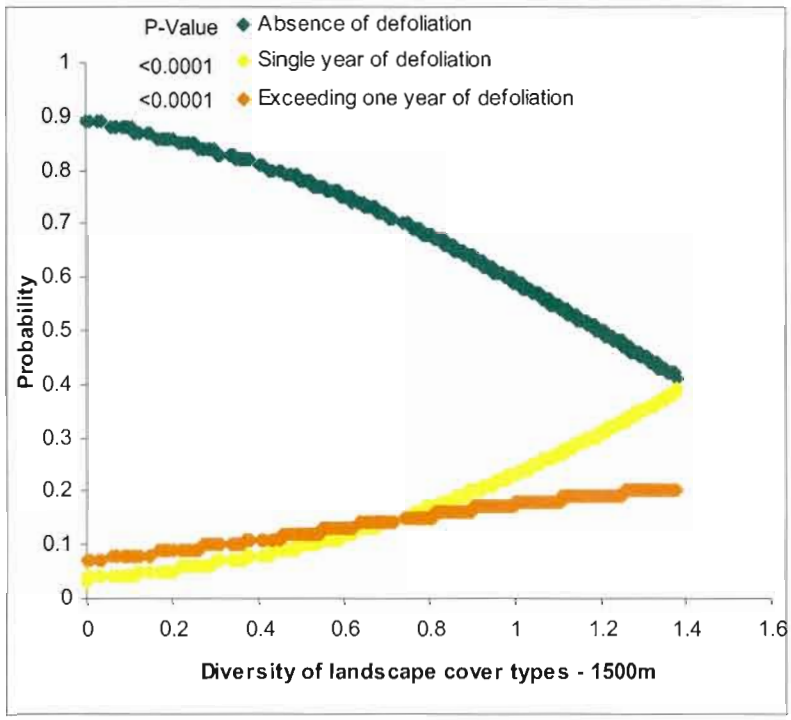


Figure 1.6 : Estimated probabilities of defoliation dynamics in relation to the diversity of landscape cover types. Probabilities were estimated through a univariate model. Parameter P-values can be found to the left of the legend

In a model building context

Adding either edge or diversity variables should result in a similar gain in predictive power. However, χ^2 values for all edge univariate models are generally low and so we would need to include more than one variable to obtain a significant change in the χ^2 value of the predictive model.

Diversity of landscape cover types provides a single variable for the final predictive model which possesses a high explanatory power, which is not redundant with the other variables selected for the model (fig. 1.7), and which will help to discriminate between the single year and multiple year defoliation dynamics.

1.3.2 Scale of landscape variable influence

The χ^2 obtained for the univariate landscape age model is very low compared to the χ^2 obtained for the stand age model. Thus, age has a greater local impact than at the landscape scale. On the other hand, cover type obtains a higher χ^2 value at the landscape scale than at the local scale. Its maximal influence is at a radius of 1500m. In fact, most of the univariate models obtain close to optimal χ^2 values at radii of 1500 m. Exceptional to this rule are the proportion of forested and non-forested stands and forested/non-forested edge which obtain maximum χ^2 values at 2000m

1.3.3 Variable classes in relation to each other

In this section, χ^2 values obtained for each individual class model as well as all possible class model combinations are illustrated (fig. 1.7). When class models are combined, a new model which includes the variables from both classes is elucidated. A χ^2 value of 411.90 is obtained for a model including all local and class variables

(12 variables in total). We consider this a baseline for comparison with our final predictive model.

It is also possible to observe relations between classes of variables. Specifically, it shows which variables are most similar and/or dissimilar to one another. For example, the contextual class model obtains a χ^2 value of 270.14. The addition of diversity variables to this model produces an increment of 16.98 (χ^2 = 287.12). Compared to the χ^2 value obtained for the model comprised of diversity variables (75.03), it seems that contextual variables and diversity variables explain a considerable portion of the same variability. On the other hand, when edge variables are added to the contextual model, an increment of 33.26 in the χ^2 value is obtained (χ^2 =303.40). Compared to the χ^2 value obtained for the edge variables model (34.84), it suggests that edge is complementary to the contextual variables in explaining the variability.

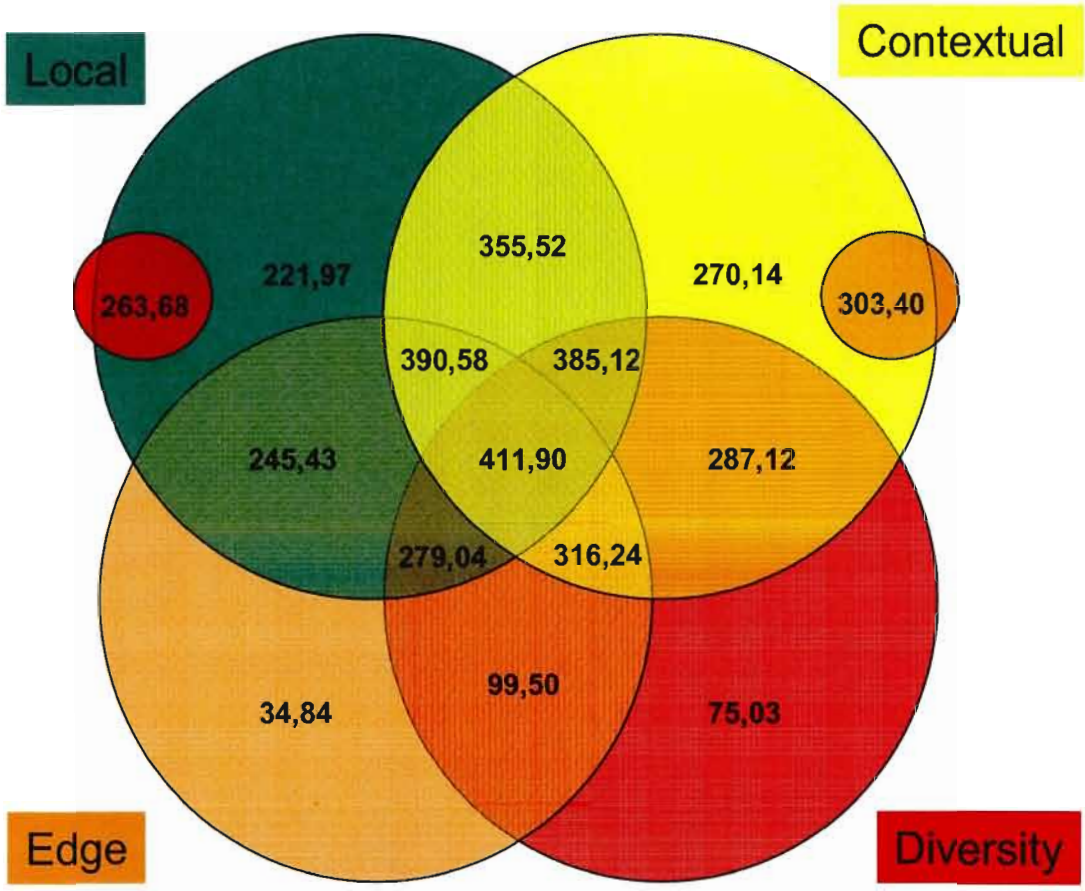


Figure 1.7 : χ^2 values obtained for each model class as well as for all possible class combinations. When two or more classes are combined, the new model includes all variables from the combined classes. The smaller red and orange ovals represent the combination of local with diversity models and edge with contextual models respectively

1.3.4 Final predictive Model

The final model includes stand age, landscape cover type and diversity of landscape cover types. Table 1.7 indicates that the model obtains a χ^2 of 326.64 and is highly significative.

Table 1.7 : χ^2 results and their probabilities obtained for the final model

Model	χ^2	*P - Value*
Landscape cover type	169.98	<0.0001
Diversity of landscape cover types	11.18	0.004
Stand Age	57.12	<0.0001
Final	**326.64**	**<0.0001**

The probabilities of individual parameter significance and odds ratios can be found in Table 1.8. Though most parameters significantly influence the probability of occurrence of the single year of defoliation and multiple years of defoliation dynamics, this is not the case for diversity of landscape cover types and the multiple years of defoliation.

Table 1.8 : Odds ratios and P-Values for individual parameters. The reference category for Stand age is 90 years, thus no P-Values or odds ratios can be calculated for this parameter.

Defoliation dynamic	Parameter		*P - Value*	O.R.
Single year of defoliation	Landscape cover type		<0.0001	0.295
	Heterogeneity of landscape cover types		0.002	3.395
	Stand age	10 yrs	0.985	1.007
		30 yrs	0.039	1.897
		50 yrs	<0.0001	4.092
		70 yrs	<0.0001	2.995
		90 yrs	.	
Exceeding one year of defoliation	Landscape cover type		<0.0001	0.114
	Heterogeneity of landscape cover types		**0.704**	**1.187**
	Stand age	10 yrs	0.496	0.726
		30 yrs	0.112	1.904
		50 yrs	<0.0001	4.752
		70 yrs	0.010	2.738
		90 yrs	.	

Influence and interaction of variables

Figure 1.8 reveals the probabilities of the defoliation dynamics in relation to the three explanatory variables included in the predictive model. Figure 1.8 a) expresses the probability of all three defoliation dynamics as a function of the landscape cover type for sample points in stands aged 10 years.

Sampled points were then separated according to their values of diversity of landscape cover types. Points with high diversity values (>1) are outlined in black, and a black trend line is added to the graph to indicate this pattern. The remaining points (≤1) are uniquely colored and have a matching trend line. This separation helps to demonstrate the influence of high diversity of landscape cover types on defoliation dynamics for a given landscape cover type and stand age. A diversity of landscape cover types value of 1 was chosen as a cutoff point because it is at this point that the probabilities of occurrence of 1 year of defoliation and multiple years of defoliation diverge (fig. 1.6). Figure 1.8 b), c), d) and e) are equivalent representations but for sample points in locally aged stands of 30, 50, 70 and 90 years, respectively.

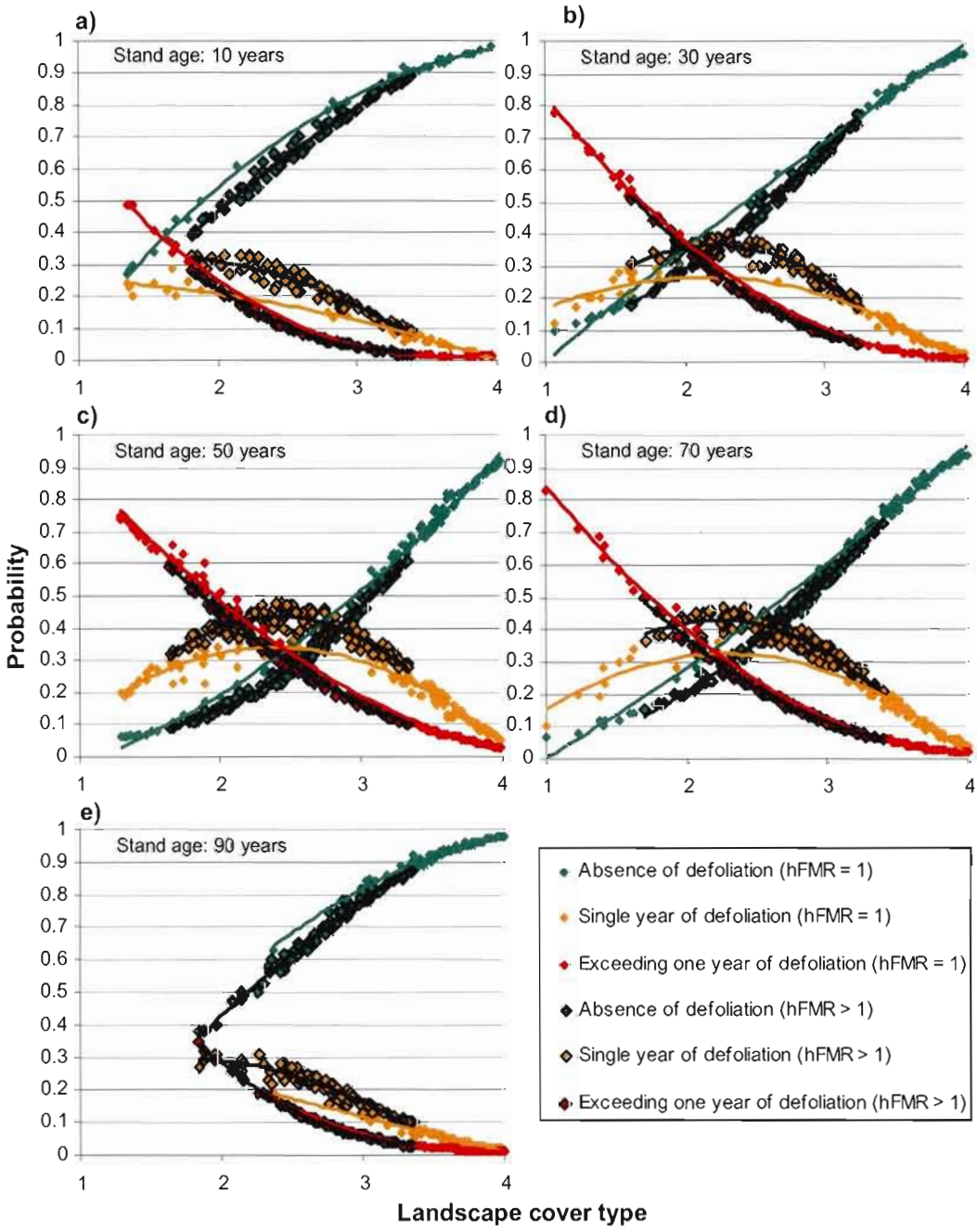


Figure 1.8 : Estimated probabilities for defoliation dynamics in relation to landscape cover type established through the final multivariate model. Sample points of each local age class have been separated into 5 separate graphs (a=10 years, b=30 years, c=50 years, d=70 years, and e=90+years). Black curves represent the variation of probability for the same defoliation dynamics for sample points of diversity of landscape cover types values greater than 1, while the colored lines represent sample points of diversity of landscape cover types values less than or equal to 1

Our results show 2 patterns of probability response according to stand age. 10 and 90 year old stands are subject to a similar probability response, which differs from the 30, 50 and 70 year stand probability response pattern (fig. 1.8).

Independently of stand age, there is a higher probability of multiple years of defoliation occurring in environments with a high proportion of deciduous species in the landscape (low landscape cover type value, Figure 1.8). In environments with a high proportion of coniferous species in the landscape, there is a high probability of there being an absence of defoliation. In landscapes where cover type is increasingly mixed, the occurring dynamic depends on stand age and diversity of landscape cover types.

When stand age is either 10 or 90 years and the landscape cover is mixed, an absence of defoliation is most probable. In 30 year stands, an absence of defoliation is the most probable dynamic for landscape cover type values of 2.3 or more. For landscape cover type values between 2 and 2.3, the likely dynamic depends on the diversity of landscape cover types, where a single year of defoliation is more likely when landscape cover types are highly diverse. For 50 and 70 year stands where the landscape cover is mixed and diversity of landscape cover types is ≤ 1, the most probable dynamic will either be multiple years of defoliation or an absence of defoliation. When diversity of landscape cover types is greater than 1, a single year of defoliation is most probable. This brings us to the effect of diversity of landscape cover types.

An increase in diversity of landscape cover types increases the probability that a single year of defoliation will occur and decreases the probability that an absence of defoliation will occur. Diversity of landscape cover types does not significantly influence the probability of occurrence of multiple years of defoliation. The influence

of this variable is strongest in mixed surrounding areas and tapers off when landscape cover type tends towards 1 or 4.

1.4 Discussion

1.4.1 Influence of variables on defoliation dynamics

Stand cover type

Results show that the probability of defoliation increases when the proportion of deciduous species in the landscape increases. The persistence of defoliation also increases when the landscape tends towards containing a high proportion of deciduous species. These effects are particularly marked at a landscape scale of 1 500 m in radius.

It has been established that deciduous hosts are preferred by the forest tent caterpillar (Batzer and Morris, 1978). In our study area, this generally means white birch or trembling aspen, the latter being more abundant. Thus, a greater proportion of deciduous species in the forest cover translates to a greater concentration of host species and consequently greater habitat quality. Ecological theory dictates that a greater habitat quality generally leads to a greater population density (Hansson *et al.*, 1995). Characteristics which are favorable to population growth will lead to a higher probability of defoliation occurrence and persistence.

Although this is not unexpected, it is interesting to note how great a role landscape cover type has in predicting defoliation dynamics. It is also very interesting to note how much greater the univariate landscape cover type model χ^2 value is compared to the local models χ^2. This indicates that landscape cover type affects local dynamics at a relatively large scale.

Despite the relationship between landscape cover type and defoliation dynamics being very clear in highly deciduous or coniferous covers, the same is not necessarily

true in mixed cover landscapes. In the latter cases, stand age and diversity of landscape cover types play a much greater role.

Age

The literature indicates that the age of host species can affect relative growth rates, leaf digestibility and conversion efficiency in insects (Bauce *et al.*, 1994; McCullough and Kulman, 1991; Donaldson *et al.*, 2006). This led us hypothesize that the probability of defoliation as well as increased defoliation persistence would be more likely as stand age increases. Our results clearly show that stands most likely to be defoliated are aged 50 and 70 years, and that persistence generally depends more on landscape cover type rather than it depends on stand age. Stands aged 10 and 90 years are the least likely to be defoliated. Thus, our initial hypothesis is disconfirmed.

Since there is very little information available on the subject, the principle basis of our hypothesis is provided by a study conducted by Donaldson *et al.* (2006), in which it is established that concentrations of secondary compounds which negatively affect forest tent caterpillar development decrease exponentially as tree age increases. However, of all six age classes considered in the Donaldson study, the oldest is an undefined 20+ year class. Since it is impossible to know from this study whether or not the relationship between tree age and foliar chemistry maintains the same exponentially decreasing function in older trees, further investigations are needed to determine if this is the mechanism responsible for the observed decrease in defoliation probability in older stands.

Of further interest, the very weak χ^2 obtained for the univariate landscape age model versus the very strong χ^2 obtained for the stand age model leads us to hypothesize that stand age affects forest tent caterpillar populations, and consequently defoliation dynamics, at a very small scale. This is particularly interesting as it is contradictory to the findings of Kouki *et al.* (1997) regarding the jack pine budworm.

Diversity of landscape cover types

Our results show that diversity of landscape cover types increases the probability that a single year of defoliation will occur, decreases the probability that an absence of defoliation will occur and has no significant influence on the probability of occurrence of multiple years of defoliation.

Bergeron *et al.* (1995) obtained similar results and reported that forest mosaic heterogeneity seems to diminish vulnerability to spruce budworm. Landscapes of mixed composition and/or structure promote a greater ecological diversity which, in turn, reduces susceptibility to pests. Indeed, a greater ecological diversity may include a greater variety and abundance of predators which will be more able to regulate forest tent caterpillar populations, thus reducing defoliation persistence.

Edge

We know that landscape fragmentation and habitat heterogeneity, as defined by Roland (1993), increases defoliation persistence. There are many hypotheses as to the mechanisms involved, but at least two of these are directly linked to the abundance of edge habitats. These are that higher solar radiation in edge habitats would lead to reduced effectiveness of the NPV (Rothman and Roland, 1998) and that differences in light regime in edge habitats could influence foliage quality and, consequently, population performance (Levesque *et al.*, 2002; Scriber and Slansky, 1981; Rossiter, 1994).

Our results clearly show that an increase in differential stand height edge and road and river edge lead to increased probabilities of defoliation. However, an increase in differential stand height edge or forested/non forested edge leads to a more rapid increase of the probability of occurrence of a single year of defoliation than that of multiple years of defoliation. Furthermore, in most cases, a single year of defoliation

is more probable than multiple years of defoliation (fig. 1.5). This seems to disagree our initial hypothesis that an increase in edge habitats would lead to an increase in defoliation persistence. However, these results do not contradict the well-established hypothesis that fragmentation increases defoliation persistence; rather it sheds some light on the importance, or lack thereof, of mechanisms related to edge habitat abundance.

In his study, Roland (1993) used the proportion of edge-to-interior habitat as a measure of fragmentation. This may be a more suitable measure of fragmentation, and would still support previous research conducted on variations in light regime and the effectiveness of the NPV virus.

It is also possible that the scale at which fragmentation is evaluated is also very important. In the course of this study, edge length is evaluated at a very fine scale and may not reflect the realities of fragmentation at the landscape scale. Indeed, when Roland (1993) establishes a relationship between fragmentation and defoliation persistence, a 4 Ha grid was used to estimate edge length and fragmentation was expressed as the ratio of edge length per km^2. Furthermore, the scale of the study area is at least 10 times greater than that considered in this study.

Though not included in the final model, border variables exert an important influence on defoliation dynamics. It would be interesting to elucidate a unified variable for edge effects that could be incorporated into the model. This variable could possibly help to better understand the role of edges habitats in the fragmentation-persistence relation.

1.4.2 Scale of landscape variable influence

Another interesting observation made in the course of this study is the various spatial scales at which various variables can influence local defoliation dynamics. On one

hand, stand age seems to have a very local effect; on the other hand, landscape cover type seems to have a maximal influence in a radius of 1500m. In fact, most landscape variables obtain close to optimal χ^2 values at radii of 1500 m. Exceptional to this rule are the proportion of forested and non-forested areas and forested/non-forested edge which obtain maximum χ^2 values at 2000m and seem to indicate that they would increase further if the radius were superior. It would appear that the interplay between forested/non-forested areas surrounding the local dynamic may have a significant influence, but possibly at a greater scale than was possible to incorporate into the scope of this study.

1.4.3 What the final model can tell us

The final predictive model helps to determine which areas are more prone to severe defoliation dynamics. Our results show that stands most likely to sustain severe defoliation are aged between 50 and 70 years and imbedded in landscapes with a high proportion of deciduous species. In mixed cover landscapes, higher diversity of cover types will increase the probability of having a single year of defoliation. With this knowledge in hand, it is possible to target areas that are more prone to severe defoliation dynamics with the goal of better managing our natural resources.

1.5 Conclusion

In this study, we sought to establish a relationship between stand attributes and spatial heterogeneity at the local and landscape scale, and the local defoliation dynamics by the forest tent caterpillar. To this end, we have utilized GIS, a specialized tool for spatial data management, and multinomial nominal logistic regressions, a type of analysis which permits us to model a system and produce probabilities of occurrence of events.

Specifically, our goal was to establish a link between defoliation dynamics and stand age and stand cover type as well the diversity of cover types and the abundance of edge habitats. In this respect, we accomplished the goals set forward by our study.

We managed to establish a strong relationship between landscape cover type and defoliation persistence. As was anticipated, an increase in the proportion of deciduous species in the landscape cover increases the probability of occurrence of multiple years of defoliation. As was also expected, an increased diversity in landscape cover types reduced defoliation persistence by increasing the probability of occurrence of a single year of defoliation in mixed cover landscapes.

However, the observed relationship between stand age and defoliation did not occur as we expected. Contrary to our initial hypothesis where an increase in stand age would increase defoliation severity, stands aged 50 and 70 years were most likely to be defoliated while stands aged 10, 30 and 90+ years were less likely. Our hypothesis in regards to the abundance of edge habitats is also disconfirmed. Our results show that a single year of defoliation is generally more probable than multiple years of defoliation in landscapes abundant in edge habitats, which contradicts our hypothesis that an increase in edge habitats would lead to an increase in defoliation persistence.

Though the goals of the study were met, we feel that some improvements are possible. These lie mostly in the evaluation of diversity and heterogeneity. A wider variety of assessments of these complex phenomena might have been preferable, such as the inclusion of species diversity within the cover or a measure of spatial distribution of stands within the area around the sample point. Furthermore, insufficient representation of areas having been defoliated three or four years imposed a grouping of 2-4 years of defoliation. It would be very interesting to see if the model could be improved if these could be considered separately.

We hope that this study is a step forward in better understanding the relationship between forest tent caterpillar defoliations and characteristics of the environments in which they inhabit. We believe that this study lays a solid foundation upon which other studies can build upon to further this aim. Furthermore, more inquiries need to be made in regards to the relationship between leaf chemistry and tree age, especially for more mature trees. We need to better understand the role of edge habitats in defoliation dynamics, perhaps through a unified edge variable that encompasses all types of edges.

As for what can be learned in regards to forest management, let us remember the convergence between the results presented here and those reported by Bergeron *et al.* (1995) where a diverse forest cover has a beneficial influence on host stand susceptibility to spruce budworm. In light of this, it would be possible to elucidate a sole forest management plan which reduces the risks of prolonged defoliations by these two insects, the forest tent caterpillar and the spruce budworm.

CONCLUSION GÉNÉRALE

Dans le cadre de ce travail, nous avons voulu établir une relation entre des caractéristiques à l'échelle locale et du paysage, et les dynamiques locales de défoliations par la livrée des forêts. À ces fins, nous avons fait usage d'un SIG, une méthode de gestion de l'information spatiale et des analyses multinomiales de régression logistique nominale, un type d'analyse qui permet d'estimer les probabilités d'occurrence de différents évènements.

Précisément, nous avons voulu établir une relation entre des dynamiques de défoliation et l'âge et le type de couvert de peuplements ainsi que la diversité des types de couverts dans le paysage et l'abondance des milieux de bordure. En cet égard, l'étude a globalement été un succès.

Nous avons établi une forte relation entre les types de couverts dans le paysage et la persistance de défoliation. Tel qu'attendu, une augmentation de la proportion d'essences feuillues dans le couvert mène à une augmentation de la probabilité d'occurrence de plusieurs années de défoliation. Également anticipé, une augmentation de la diversité des types de couverts dans le paysage réduit la persistance de défoliation en augmentant la probabilité d'occurrence d'une seule année de défoliation.

Toutefois, la relation observée entre l'âge des peuplements et les dynamiques de défoliation ne se sont pas manifestées telles que nous pensions. Contrairement à notre hypothèse de départ où une augmentation de l'âge des peuplements augmenterait l'intensité et la persistance des défoliations, nous observons que les peuplements âgés de 50 et 70 ans sont les plus probables d'être défoliés tandis que les peuplements âgés de 10, 30 et 90+ ans sont moins probables. Notre hypothèse au niveau de l'abondance des milieux de bordure est également rejetée. Nos résultats indiquent qu'une seule

année de défoliation est plus probable que plusieurs années, ce qui contredit notre hypothèse qu'une augmentation de l'abondance des milieux de bordure mènerait à une augmentation de la persistance de défoliation.

Bien que l'étude soit globalement un succès, nous croyons que certaines améliorations sont possibles. Ceux-ci résident surtout au niveau des méthodes de quantification de la diversité et de l'hétérogénéité. Une plus grande variété de variables caractérisant ces phénomènes complexes pourrait être préférable. Il aurait été possible d'inclure la diversité en espèces dans le couvert forestier ou même ajouter une mesure de la répartition spatiale des peuplements à l'intérieur des aires échantillonnées. De plus, vue la faible représentativité des milieux ayant été défoliés 3 ou 4 ans, nous avions dû grouper les aires ayant été défoliés de 2 à 4 ans. Il serait fort intéressant de voir si une évaluation individuelle de chaque année de persistance améliorerait significativement le modèle prédictif.

Néanmoins, nous avons pu mener à terme une étude fort intéressante qui nous permet de mieux prédire les dynamiques de défoliation de la livrée et qui ouvre les portes sur plusieurs avenues de recherche futures fort intéressantes. De plus, nous avons un aperçu des autres facteurs susceptibles d'influencer les dynamiques de défoliation, notamment l'abondance de bordures et l'interaction entre les milieux forestiers/non forestiers à très grande échelle.

Nous espérons que cette étude soit un premier pas vers une compréhension accrue de la relation entre les dynamiques de défoliations causées par la livrée des forêts et les caractéristiques des milieux qu'elle habite. Nous croyons que cette étude pose une solide fondation sur laquelle des études subséquentes pourront construire et poursuivre ce but. De plus, les questions soulevées au cours de cette étude requièrent une attention particulière. Entre autres, une meilleure compréhension de la relation entre l'âge et la chimie foliaire du peuplier faux-tremble, particulièrement chez les

individus plus âgés. Nous devons également mieux comprendre le rôle que jouent les milieux de bordure dans les dynamique de défoliations, possiblement à l'aide d'une variable de bordure unifiée qui engloberait plusieurs types de bordures.

De plus, une meilleure compréhension de la façon dont se matérialise l'interaction entre la dynamique de l'insecte et la composition forestière ont un intérêt économique certain. Elles permettraient d'établir un plan d'aménagement en fonction de la dynamique spatiotemporelle de la livrée, où les situations menant à la mortalité du peuplier, notamment des périodes de défoliation prolongécs, pourraient êtres évitées.

Rappelons aussi la convergence entre les résultats présentés ici et ceux rapportés par Bergeron *et al.* (1995) au sujet de l'influence bénéfique de la diversité du couvert sur la diminution de la susceptibilité des peuplements hôtes de la tordeuse des bourgeons de l'épinette. Ceci implique qu'il est possible d'envisager un seul et même aménagement pour réduire les risques de défoliations prolongées par ces deux insectes.

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